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Predicting the potential distribution area of *Solidago ×niederederi* (Asteraceae)

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Abstract: In this study, we aimed to investigate the potential distribution area of *Solidago ×niederederi*, a natural hybrid between North American *S. canadensis* and European *S. virgaurea*, in Central and East Europe using the MAXENT modeling approach. The final MAXENT model was constructed based on 83 occurrence records from Austria, Poland, Lithuania, and Latvia and six abiotic environmental variables. The jackknife test revealed that annual temperature range, mean temperature of wettest quarter, and minimum temperature of coldest month had the highest gain for the training and test data when used alone, whereas precipitation seasonality, precipitation of coldest quarter, and precipitation of warmest quarter reduced the gain the most when excluded from the model and thus contributed the most information not presented with the other variables. A high probability of occurrence (>0.6) for *S. ×niederederi* was found in 12 countries, namely Austria, Belarus, the Czech Republic, Germany, Hungary, Italy, Lithuania, Poland, Russia (Kaliningrad Oblast), Slovenia, Slovakia, and Ukraine. Our results showed in which areas the hybrid may be established under the European temperate climatic conditions; however, we do not indicate which areas exactly may be under invasion by the hybrid because such a statement needs population dynamic data for proper investigation. To prevent the negative impact of *S. ×niederederi* on native *S. virgaurea* (i.e. competition for pollinators and introgression) we suggest that it should be controlled first in areas of high probability of occurrence, especially in Lithuania, Kaliningrad Oblast, Slovakia, Poland, and Austria, where the areas of high probability of hybrid occurrence account for more than 5% of the territory concerned.

Key words: Alien species, plant hybridization, species distribution modeling, MAXENT

1. Introduction

Natural hybrids between alien and native plant species are usually found in areas of overlapping ranges of their parental species. If they are viable and able to reproduce and spread, they can create their own geographical ranges, sometimes totally different from the ranges of one or both parental species, such as a hybrid between *Spartina alternifolia* Loisel. and *S. maritima* (Curtis) Fernald that gave rise to *S. anglica* C.E. Hubb. (Ayres and Strong, 2001; Daehler and Carino, 2001; Stace et al., 2015). It was suggested by Pyšek et al. (2004) that hybrids between alien and native plants should be treated as alien species because they arise in areas where geographical and ecological barriers have been broken by human activities, and as a consequence they can be considered as casual, established, or invasive species. From the conservation point of view, predicting geographical distribution of such hybrids is a first step in controlling their further spreading. Various modeling methods (heavily based on climatic data) have been used to predict distribution areas of naturalized or invasive plant species (e.g., Pattison and Mack, 2008; Qin et al., 2015; Wang and Xu, 2016). Unfortunately, there is a lack of study on modeling potential geographical distribution for hybrids between alien and native plant species that have the ability to produce their own offspring and become established.

Solidago ×niederederi Khek (Asteraceae) was described from Austria as a natural hybrid between North American *S. canadensis* L. s. l. and European *S. virgaurea* L. s. str. at the beginning of the 20th century (Pliszko, 2015; Pliszko and Zalewska-Gałosz, 2016). Aside from the Austrian records, the hybrid has been reported from Italy, the United Kingdom, Denmark, Sweden, Norway, Germany, Poland, Lithuania, Latvia, and Russia; however, its geographical distribution is poorly recognized (Nilsson, 1976; Burton, 1980; Sunding, 1989; Mayorov et al., 2012; Pliszko, 2013, 2015; Stace et al., 2015; Gudžinskas and Petrulaitis, 2016; Karpavičienė and Radušienė, 2016; Pliszko and Zalewska-Gałosz, 2016). It appears that *S. ×niederederi* is formed easily wherever the parental species grow in proximity, mainly in anthropogenic habitats such as abandoned fields, roadsides, railway embankments, disused quarries, and

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tree plantations (Nilsson, 1976; Pliszko, 2013, 2015; Stace et al., 2015). Taking into account the wide native range of *S. virgaurea* s. str. (Slavík, 2004; Kiełtyk and Mirek, 2014) as well as the wide naturalized range of *S. canadensis* s. l. in Europe (Greuter, 2006; Kabuce and Priede, 2010), the hybrid is almost certainly underrecorded in some areas. In addition, recent data from Austria, Poland, and Lithuania suggest that the hybrid is much more frequent than previously thought (Viltrakytė and Karpavičienė, 2014; Pagitz and Lechner-Pagitz, 2015; Gudžinskas and Žalneravičius, 2016; Karpavičienė and Radušienė, 2016). *Solidago ×niederederi*, which is a perennial plant, forms vigorous and often persistent clonal clumps of stems, similar to those observed in its parental species. It reproduces generatively by wind-dispersed achenes; however, the number of well-developed fruits is low in the hybrid (Nilsson, 1976), which seems to be caused by its reduced pollen viability (Migdałek et al., 2014). There is no evidence that the hybrid (at least the F_1 generation) forms long rhizomes typical of *S. canadensis*. The vegetative reproduction of *S. ×niederederi* has not been separately studied; however, the fragmentation of its clonal clumps of stems by wild animals (e.g., wild boar rooting) and human activities (e.g., construction and modernization of roads) is highly probable. Furthermore, field observations in Poland suggest that the hybrid attracts many pollinators and therefore can pose a threat to native *S. virgaurea*, since its pollination biology, which is mainly based on self-incompatibility (Nilsson, 1976), promotes backcrossing and introgression. The negative impact of the hybrid on native biodiversity requires a thorough study. In this paper, we aimed to investigate the potential distribution area of *S. ×niederederi* in Central and East Europe using the MAXENT model, a widely applied species distribution modeling (SDM) tool (Fourcade et al., 2014).

2. Materials and methods

2.1. *Solidago ×niederederi* records

In order to predict the potential distribution of *Solidago ×niederederi* in Central and East Europe with the MAXENT model we decided to use the records from Austria, Poland, Lithuania, and Latvia, where the hybrid is well recognized by specialists and considered an established alien species and, most importantly, where its distribution is supported by adequate GPS data. Therefore, we selected a total of 83 records (GPS coordinates in the WGS84 system), keeping a minimum distance of 1 km between hybrid occurrence points. The records from Austria and Latvia were obtained from the literature (Pagitz and Lechner-Pagitz, 2015; Gudžinskas and Petrulaitis, 2016), whereas those from Poland were gathered from field surveys conducted by Artur Pliszko in 2013–2016. The records from Lithuania were contributed by Birutė Karpavičienė in accordance with published data (Viltrakytė and Karpavičienė, 2014; Karpavičienė and Radušienė, 2016). The hybrid was identified based on morphological characters provided by Nilsson (1976) and Gudžinskas and Žalneravičius (2016).

2.2. MAXENT modeling

MAXENT is a generative species distribution modeling approach recommended for applications involving presence-only datasets. It allows for estimating a target probability by finding the probability distribution of maximum entropy using presence localities together with environmental data (Phillips et al., 2006). It is important that the algorithm based on maximum entropy is considered less sensitive to sample size than other methods used in SDM (Wisz et al., 2008). This method was successfully used in many ecological and biogeographical studies (de Araújo et al., 2014; Holzmann et al., 2015; Qin et al., 2015). For modeling the potential distribution of *Solidago ×niederederi* in Central and East Europe we used MAXENT software version 3.3.3 k. It was run with a maximum of 500 iterations, convergence threshold 0.00001, and all five auto feature classes (which are default values). It generated logistic outputs showing potential occurrence suitability for species on a scale of 0–1. We decided to choose a logistic format, as it is currently considered easier and potentially more accurate for interpretation than the cumulative and raw approaches (Phillips and Dudík, 2008; Baldwin, 2009). As a threshold rule, we applied the minimum training presence (MTP). The model was calibrated using 75% of the occurrence records and tested on the remaining 25%. We performed 10 replicates using the subsample replicated run type and then averaged the results. To provide a different random test/train partition in each replicate, we used the "random seed" option. We evaluated the final model using the area under the curve (AUC) values, which is a threshold-independent evaluation analysis (Phillips et al., 2006) generated automatically by MAXENT.

To develop a species distribution model, we used information derived from the WorldClim 1.4 database at a spatial resolution of 30 arcseconds (Hijmans et al., 2005; available online: http://www.worldclim.org/). The initial model was run using 19 bioclimatic variables collected between 1960 and 1990, namely annual mean temperature (bio1), mean diurnal range of temperature (bio2), isothermality (bio3), temperature seasonality (standard deviation × 100) (bio4), maximum temperature of warmest month (bio5), minimum temperature of coldest month (bio6), annual temperature range (bio7), mean temperature of wettest quarter (bio8), mean temperature of driest quarter (bio9), mean temperature of warmest quarter (bio10), mean temperature of coldest quarter (bio11), annual precipitation (bio12), precipitation of wettest month (bio13), precipitation of driest month (bio14), precipitation seasonality (coefficient of variation) (bio15), precipitation of wettest quarter (bio16), precipitation of driest quarter (bio17), precipitation of warmest quarter (bio18), and precipitation of coldest quarter (bio19), as well as altitude (alt16). To avoid overfitting of the model we built a correlation matrix (Pearson's correlation coefficient) and excluded highly correlated variables (r > 0.7). To decide which of the highly correlated variables should be left in the model, we used the jackknife test of variable importance, eliminating variables that showed low or negative gain values (Baldwin, 2009). In the final model, therefore, we used six abiotic environmental variables, namely minimum temperature of coldest month, annual temperature range, mean temperature of wettest quarter, precipitation seasonality (coefficient of variation), precipitation of warmest quarter, and precipitation of coldest quarter.

3. Results

The high values of AUC for the training (0.970) and test (0.965) data confirmed that the final model is able to predict the areas of *Solidago ×niederederi* presence. The jackknife test showed that in the final model formed with six environmental variables, annual temperature range, mean temperature of wettest quarter, and minimum temperature of coldest month had the highest gain for the training and test data when used alone (Table). Precipitation seasonality, precipitation of coldest quarter, and precipitation of warmest quarter reduced the gain the most when excluded from the model and thus contributed the most information not presented with the other variables (Table). A high probability of hybrid occurrence (>0.6) is reached when annual temperature range exceeds 18 °C and continues to grow as the temperature rises to a value of 30 °C. The probability of occurrence of *S. ×niederederi* rapidly increases at the mean temperature of wettest quarter, reaching about 15 °C. The probability of hybrid presence increases with decreasing temperature of coldest month (i.e. when the temperature drops to −10 °C, the probability is almost full, but when it reaches a value of about 0 °C, it is equal to zero). The occurrence of *S. ×niederederi* decreases with decreasing values of precipitation seasonality and precipitation of coldest quarter, but increases with increasing precipitation of warmest quarter.

A high probability of occurrence (>0.6) for *S. ×niederederi* was found in areas located in 12 countries, namely Austria, Belarus, the Czech Republic, Germany, Hungary, Italy, Lithuania, Poland, Russia (Kaliningrad Oblast), Slovenia, Slovakia, and Ukraine (Figure). Moreover, a lower, but noteworthy, probability of hybrid occurrence (0.2–0.6) was predicted in some areas located in another five countries, namely Croatia, Denmark, Latvia, Switzerland, and Romania. Considering the part of Europe shown in the Figure, areas of high potential (>0.6) accounted for 2.7% of the total land presented, whereas areas of very low potential (<0.2) accounted for 83.9%. With respect to the country concerned, the largest areas of high probability of hybrid occurrence (>0.6) were found in Lithuania (15.8%), Slovakia (7.3%), Poland (5.4%), and Austria (5.0%). Moreover, in Russian Kaliningrad Oblast, the area of high probability of hybrid occurrence was also large and accounted for 14.0%.

4. Discussion

In this study, regarding the current distribution of *Solidago ×niederederi* in Europe (Gudžinskas and Petrulaitis, 2016; Pliszko and Zalewska-Gałosz, 2016), we revealed that the areas of high probability of occurrence are in countries

Table. Results of the jackknife test for evaluating the relative importance of environmental variables for *Solidago ×niederederi* distribution in Central and East Europe.

Environmental variable	Abbreviation*	Training data		Test data	
		Gain with only variable	Gain without variable	Gain with only variable	Gain without variable
Precipitation seasonality (coefficient of variation)	bio15	0.399	2.157	0.444	2.403
Precipitation of warmest quarter	bio18	0.407	2.069	0.529	2.293
Precipitation of coldest quarter	bio19	0.285	2.098	0.314	2.351
Minimum temperature of coldest month	bio6	0.647	1.945	0.778	2.240
Annual temperature range	bio7	0.936	1.619	1.071	1.955
Mean temperature of wettest quarter	bio8	0.744	1.733	0.843	2.120

*After WorldClim 1.4 database.

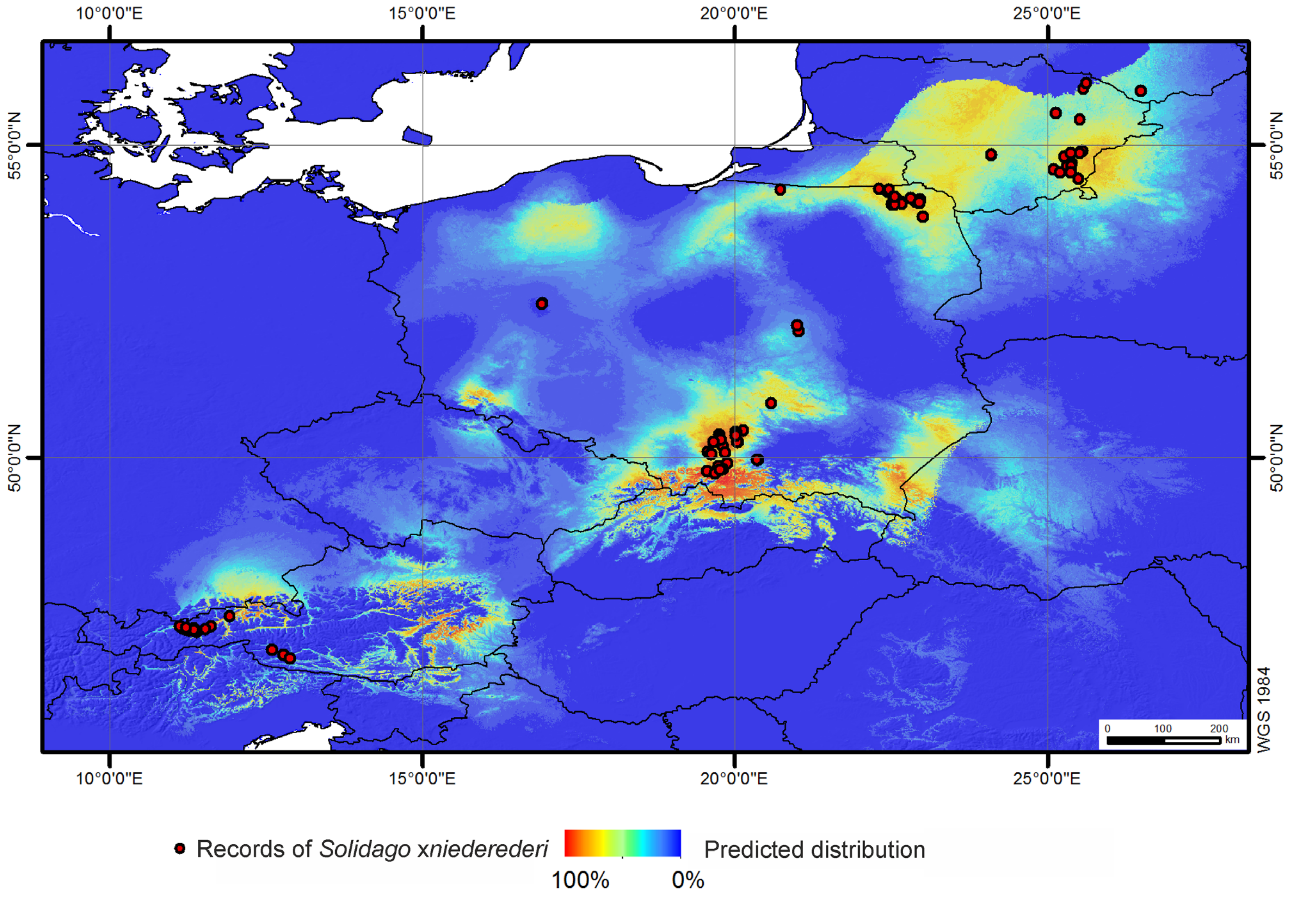

Figure. Map of potential distribution of *Solidago ×niederederi* in Central and East Europe derived from MAXENT.

from which the hybrid has not been reported so far (i.e. Belarus, the Czech Republic, Hungary, Slovakia, Slovenia, and Ukraine). Taking into consideration that both parental species occur in the aforementioned countries (Greuter, 2006; Kabuce and Priede, 2010), it is intriguing to test the predicted areas of hybrid extension in the field. Moreover, we revealed new areas of high probability of occurrence in countries in which the hybrid has been confirmed (e.g., Kaliningrad Oblast in Russia, Sudety Foothills in Poland). To be more critical of our results, we realized that the map derived from the MAXENT model (Figure) seems to be a restrictive prediction due to the relatively low number of presence-occurrence records included. However, adequate GPS records of hybrid occurrence are still limited in publications. On the other hand, some points of hybrid occurrence (e.g., in Poznań, northeastern Poland) presented extreme values of the most important climatic variables and were treated by the model as divergent. As a result, the probability of hybrid occurrence at these points was very low (Figure). Moreover, we stated that climatic conditions are the most influential factors determining hybrid establishment, excluding habitat variables (e.g., pH and soil moisture). However, soil preferences of *S. ×niederederi* are poorly recognized and need to be intensively studied. We also excluded the occurrence of the parental species from the model. Nevertheless, during field surveys in Poland numerous localities were evidenced in which *S. canadensis* and *S. virgaurea* cooccurred with no sign of hybrid presence, as well as a few localities in which the hybrid was found alone or with one parental species.

Focusing on the jackknife test results, we would like to emphasize that two environmental variables, namely mean temperature of wettest quarter and precipitation seasonality (coefficient of variation), were also revealed by the MAXENT model as the most important factors in determining the potential distribution of *S. canadensis* in China (Xu et al., 2014). Moreover, the strong influence of the minimum temperature of coldest month on *S. ×niederederi* occurrence in Central and East Europe confirms the known regularity in plant species distribution (Woodward and Williams, 1987; Ashcroft et al., 2010). The above-mentioned variables, as well as annual temperature range, precipitation of warmest quarter, and precipitation of coldest quarter, indicate favorable conditions for plant growth and photosynthesis (Xu et al., 2014). We assumed that most likely the minimum temperature of coldest month, annual temperature range, mean temperature of wettest quarter, precipitation seasonality (coefficient of variation), precipitation of warmest quarter, and precipitation of coldest quarter influence the hybrid fruit set, seed germination, and seedling recruitment, which are essential for its establishment. Furthermore, in our study, altitude was highly correlated with other variables and thus we excluded it from the final model. However, the distribution of *S. ×niederederi* along the altitudinal gradient in Europe seems to be an interesting subject for further study on its establishment and invasive potential. According to Pagitz and Lechner-Pagitz (2015), some of the highest elevations reached by the hybrid were registered in the Alps (e.g., 885 m a.s.l. in Natters, North Tyrol and 875 m a.s.l. in Grafendorf, East Tyrol, Austria). In the Carpathians, the occurrence of *S. ×niederederi* is poorly recognized and its highest known locality is situated at 567 m a.s.l. in Budzów near Jachówka, Western Beskids, Poland.

Due to progressive invasion of *S. canadensis* in Europe during the last few decades (Kabuce and Priede, 2010), spontaneous hybridization between *S. canadensis* and *S. virgaurea* became a more common process, and *S. ×niederederi* started creating its own geographic range, which seems to be strongly related to areas of overlapping ranges of its parental species. At the same time, it should be pointed out that theoretically the hybrid can arise in every area occupied by its parental species, but its persistence and establishment are limited by climatic and habitat conditions. Our results suggest in which areas *S. ×niederederi* may be established under the European temperate climatic conditions; however, we do not indicate which areas exactly may be under invasion by the hybrid because such a statement needs population dynamic data for proper investigation (Pyšek et al., 2004). The predicted geographical distribution of the hybrid in Central and East Europe reflects its early range of naturalization, which is typically clustered. To prevent the negative impact of *S. ×niederederi* on *S. virgaurea* (i.e. competition for pollinators and introgression) we suggest that it should be controlled first in areas of high probability of occurrence, especially in Lithuania, Kaliningrad Oblast, Slovakia, Poland, and Austria, where the areas of high probability of hybrid occurrence account for more than 5% of the territory concerned. To eliminate or slow down the process of hybrid establishment, we also suggest control of *S. canadensis* in areas shared with *S. virgaurea*. From the conservation point of view, it is worth mentioning that areas of high probability of hybrid occurrence are located in some national parks (e.g., Trakai National Park in Lithuania, Wigry National Park in Poland, and National Park Kalkalpen in Austria). Finally, we think that the map derived from the MAXENT model is a useful prediction tool for further studies on *S. ×niederederi* occurrence in Europe.

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